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OBSERVATIONS ON THE TAXONOMY AND NATURAL HISTORY OF *OPHRAELLA* WILCOX (COLEOPTERA: CHRYSOMELIDAE), WITH A DESCRIPTION OF A NEW SPECIES

Douglas J. Futuyma

Department of Ecology and Evolution,
State University of New York at Stony Brook,
Stony Brook, New York 11794

Abstract.—Morphological evidence indicates that the North American galerucine genus *Ophraella* is a strictly monophyletic taxon, closely related to *Monoxia* LeConte and *Erynephala* Blake. Host associations for all species, including several hitherto lacking host records, are listed; all hosts are in the Asteraceae. Distinguishing morphological features of adults are described, and descriptions of immature stages of most of the species are provided. *O. macrovittata* LeSage is placed in synonymy with *O. sexvittata* (LeConte), and the possibility of conspecificity of *O. pilosa* LeSage and *O. americana* (Fabricius) is raised. A new species, *Ophraella artemisiae,* is described from Texas.

Several features of the life history are described. Phenological data indicate that northern populations and species are univoltine, whereas more southern populations are generally multivoltine. Cocoon formation differs from previous reports in that the cocoon material issues from the rectum. Several natural enemies were observed, including, in *O. communa* LeSage, a eulophid genus not previously recorded in North America. Geographically isolated populations of *O. communa* display partial sexual isolation, as do closely related sympatric species (*O. communa* and *O. notulata* [Fabricius]) which occupy different host plants. A difference in host affiliation is therefore not the only barrier to gene exchange.

Species of *Ophraella* Wilcox, a North American genus of leaf beetles (Chrysomelidae: Galerucinae, tribe Galerucini), are locally abundant throughout much of their range. Nevertheless, little is known of the biology of the genus, perhaps because the host plants have little economic importance. A few comments on host associations and other aspects of the biology of some species are provided by Blatchley (1910), Woods (1924), Wilcox (1965), Messina and Root (1980), and LeSage (1986); the life history of only one species has been described in any detail (Welch, 1978; Goeden and Ricker, 1985). The genus was revised by LeSage in 1986.

In the course of an ongoing analysis of the phylogeny and of the evolution and genetics of host association in the genus, I have made a variety of observations that increase the taxonomic and biological knowledge of *Ophraella.* Although some of these observations are not quantitative, investigators embarking on the study of little known taxa will find qualitative observations more helpful than none at all. In subsequent publications I shall treat the morphology of *Ophraella* and related genera, and the phylogeny and evolution of host associations within the genus, based on morphological and electrophoretic analyses. In another publication (Futuyma, in press), I have described feeding responses of many of the species to their congeners' host plants.

MONOPHYLY OF *OPHRAELLA*

Wilcox (1965) segregated *Ophraella* from *Galerucella,* and considered it most closely related to *Erynephala* Blake, *Monoxia* LeConte, *Ophraea* Jacoby, and several Neotropical genera. White (1979) referred the Neotropical *Trirhabda dilatipennis* Jacoby to *Ophraella,* but LeSage (1986) later placed this species in *Neolochmaea* Laboissiere. I have examined the morphology of this species, as well as species of *Erynephala, Monoxia,* and the holarctic taxon *Pyrrhalta* (subgenus *Tricholochmaea*) Laboissiere.

With reference to *Neolochmaea* and *Pyrrhalta,* the close relationship of *Ophraella* to *Monoxia* and *Erynephala* is supported by several synapomorphies not hitherto noted, including (1) spermathecal duct inserted subbasally (rather than extending rectilinearly from base); (2) sternum VIII of the female lacking the long anterior rod-like apodeme present in the other genera; (3) styli of the female (referred to as "accessory glands" by LeSage (1986)) reduced to flat setiferous discs (rather than elongate); (4) internal sac of male lacking ornamentation; (5) internal scuto-scutellar sclerites of larva each bearing laterally what appears to be a setaless socket (absent in the other genera). Brivio (1977) has noted that the above differences in female genitalia between *Ophraella* and *Pyrrhalta* also distinguish *Ophraella* from *Galerucella* (s.s.) and, for the most part, from *Xanthogaleruca. Ophraella* shares with *Monoxia,* its apparent sister group, the following synapomorphies: (1) pupation within a loosely woven cocoon rather than free; (2) sternum VIII of female with lateral extensions of the base (absent in the other genera); (3) apex of the male sternum deeply, conically invaginated (vs. shallowly or not at all); (4) aedeagus (median lobe) basally with a dorsal ring (vs. absent), this laterally confluent with the basal spurs. In addition to the features noted by LeSage (1986), the species of *Ophraella* share the following synapomorphic characters with respect to the condition in *Erynephala* and *Monoxia*: (1) mandible of adult with three rather than five teeth; (2) teeth IV and V of larval mandible only shallowly (rather than fully) separated, hence appearing fused basally; (3) larval cuticle lacking discrete aggregations of pigment ("melanophores"); (4) setae of dorsal sclerites of larva almost uniform in length (strongly variable in the other genera). Electrophoresis of 18 enzyme loci also supports the monophyly of *Ophraella* relative to *Monoxia* and *Erynephala* (Futuyma and McCafferty, in prep.).

TAXONOMY AND HOST AFFILIATION

LeSage (1986) recognized 13 species of *Ophraella,* of which he described five as new, renaming two others. He listed host records for 11 species. My records confirm LeSage's (1986) and Wilcox's (1965) supposition that all the hosts of *Ophraella* are Asteraceae (Compositae) (Table 1). Below I present an account of my present understanding of the taxonomic status and host affiliation of each of the species.

(1) *O. americana* (Fabricius) and *O. pilosa* LeSage. LeSage reported host records for *O. americana* as "*Solidago* spp.," and distinguished *O. pilosa* from *O. americana* on the basis of slight differences in genitalia, markings, average body size, the density of erect setae on the elytra, and association with *Aster.* Collections from *Aster* species (especially *A. urophyllus*) in central New York, Missouri (Dade Co.), Montana (Lake Co.), and Ontario (Leeds Co.) all conform morphologically to the description of *O. pilosa.* I have collected these forms on *Solidago* only in Ithaca, New York, where

Table 1. Known host plants of *Ophraella* species. Notations following host records: L, literature records (cf. LeSage, 1986; Goeden and Ricker, 1985); P, personal record; *, host not previously reported. Localities for host records are indicated in some instances. Attributions to other collectors are based on reliable personal communications.

Species	Known hosts
O. americana[1]	*Solidago* sp. (L)
O. pilosa[1]	*Aster macrophyllus* (L, P), *A. cordifolius* (L), *A. paniculatus* (L), *A. urophyllus* (P*, N.Y., Mo.), *A. laevis* (P*, Mt.), *A. lowrieanus* (P*, N.Y.), *A. novae-angliae* (H. Damman*, Ont.), *Solidago bicolor* (P*, N.Y.), *S. squarrosa* (R. Hamilton*, N.Y.)
O. notata	*Eupatorium perfoliatum* (L, P), *E. maculatum* (P*, N.Y.), *E. hyssopifolium* (P*, Va.), *E. capillifolium* (E. Hoebeke*, Fl.)
O. cribrata	*Solidago juncea* (L, P), *S. altissima* (L, P), *S. nemoralis* (L), *S. pinetorum* (P*, Va.), *S. bicolor* (P*, N.Y.)
O. conferta[1]	*Solidago altissima* (L, P), *S. gigantea* (P*, N.Y.), *S. juncea* (P*, N.Y.), *S. canadensis* (L), *S. rugosa* (L, P)
O. sexvittata (and *O. macrovittata*)[1]	*Solidago altissima* (P*), *S. leavenworthii* (P*), *S. gigantea* (J. Sullivan*, Mo.)
O. arctica	*Solidago multiradiata* (L, P)
O. bilineata	*Chrysopsis villosa* (L, P)
O. nuda	*Iva axillaris* (P*)
O. californiana	*Artemisia Douglasiana* (L)
O. artemisiae	*Artemisia Carruthii* (P*), *A. ludoviciana* (L)
O. notulata	*Iva frutescens* (L, P), *I. annua* (P*, La.)
O. communa	*Ambrosia artemisiifolia,* (L, P), *A. psilostachya* (L), *Iva axillaris* (R. Goeden*, P*, Ca.), *Xanthium strumarium* (L), *Helianthus ciliaris* (P*, Tx.), *Ratibida pinnata* (J. Sullivan*, Mo.)

[1] See text regarding taxonomic status.

larvae were taken on *Solidago bicolor, Aster macrophyllus,* and *A. Lowrieanus,* growing intermingled. These specimens, reared to adulthood, show no host-associated differences in the characters given by LeSage. Within *O. pilosa* taken from *Aster urophyllus* in New York, the range of intraspecific variation equals or exceeds the reported difference between *O. americana* and *O. pilosa* for the following characters held to distinguish these taxa: form of coronal marking (linear vs. triangular), form of spermathecal receptacle (ovoid vs. rounded), breadth/length of stalk of sternum VIII of female. (These characters are also intraspecifically variable in other species of *Ophraella.*)

Evidence of reproductive isolation between sympatric populations (the definition of biological species) can be provided not only by morphological differences, but also (and often more reliably) by substantial differences in allele frequencies at individual loci. In the limit, the absence of heterozygotes for pairs of alleles that are restricted to different populations provides conclusive evidence that the populations are different species. Loci identified by enzyme electrophoresis have proven useful in discriminating sibling species (e.g., Grassle and Grassle, 1976; Bush and Kitto, 1978). The electrophoretic data reported here and the methods used (Harris and Hopkinson, 1976) will be presented in full in a future paper (Futuyma and McCafferty, in prep.).

Allele frequencies in the syntopic collection of *O. americana*-like specimens from *Solidago bicolor* and *Aster* in Ithaca (combining samples from 1 June 1987 and 21 June 1988) did not differ at 11 fixed or 6 variable loci (N = up to 49 and 66 genes for *Solidago* and *Aster* samples respectively). At one locus (6PGD, E.C.1.1.1.44), allele frequencies differed significantly ($\chi^2 = 7.516$, df = 2, $P < 0.025$) between samples from *Solidago* (allele frequencies $p_1 = 0.07$, $p_2 = 0.62$, $p_3 = 0.31$; N = 30 genes) and *Aster* ($p_1 = 0.34$, $p_2 = 0.52$, $p_3 = 0.14$; N = 30 genes; p_3 = the summed frequency of four rarer alleles).

Larvae taken from *Solidago* and *Aster* at the Ithaca site on 21 June 1988 were reared to adulthood on *Solidago bicolor* and *Aster urophyllus* respectively, and tested individually for their feeding preference between these plants. Each beetle was placed in a 100-mm-diameter dish with moist filter paper and a leaf of each species, in a 14:10 L:D, 25°C/20°C incubator at 85% RH for two days; the foliage was replaced after 24 hr, and feeding in each 24-hr period was scored as the leaf area consumed (measured under a microscope with a rectangular ocular grid). Of 58 animals tested, 12 had been exposed to the rearing host between eclosion and testing; these did not differ in preference from the "naive" animals. Using total consumption of each plant, 13 of 23 *Aster*-derived beetles preferred *Aster* and 27 of 35 *Solidago*-derived animals preferred *Solidago,* a significant association ($\chi^2 = 6.803$, df = 1, $P < 0.01$). Considered separately, significantly more beetles from *Solidago* preferred *Solidago* ($\chi^2 = 10.314$, df = 1, $P < 0.005$), whereas those from *Aster* displayed no significant preference ($\chi^2 = 0.391$).

Only the allele frequency at one locus, and the apparent difference in breadth of host acceptability, suggest the possibility of a host-associated subdivision of this population into "host races" (Jaenike, 1981; Diehl and Bush, 1984; Futuyma and Peterson, 1985) or species. Whether or not *O. pilosa,* which according to LeSage (1986) is distributed primarily in northern United States and southern Canada, is specifically distinct from *O. americana* is uncertain at this time. In the collections I have examined, specimens most readily referred to *O. americana* by their high density of erect elytral setae are mostly from the southern U.S. Whether this represents geographic variation or the existence of two species cannot be determined until differentiation between sympatric populations is demonstrated.

Specimens of *O. americana/pilosa* can be distinguished from other species of *Ophraella* by the characters noted by LeSage, as well as by the greater number of setae on the penultimate segment of the labial palp (>2) and on the ligula (>4), extremely stout marginal setae on the ventral lobe of the lacinia, and by larval and pupal characters (see below).

(2) *O. notata* (Fabricius). A very distinct species (see LeSage, 1986), which resembles the "communa group" (see below) in size and elytral pattern, but is more similar to *O. cribrata* and *O. sexvittata* in several morphological respects (e.g., obsolescent gular sutures, strongly inflexed tooth I of mandible, deeply cleft lacinia, form of the spermatheca, and larval characters noted below). It is by far most abundant on *Eupatorium perfoliatum* in northeastern U.S., but I have found small numbers of adults and eggs on *E. maculatum* associated with *E. perfoliatum* (Ithaca, N.Y.) and have taken adults on *E. hyssopifolium* in Virginia (Mecklenburg Co.). Adults and larvae have been found on *E. capillifolium* in Hernando Co., Florida (Cornell University: E. R. Hoebeke).

(3) *O. cribrata* (LeConte). Morphologically similar to *O. conferta* except in those characters noted by LeSage (1986), the status of this species is not in doubt. I have collected it on *Solidago juncea* at many localities in the northeastern U.S., on *S. pinetorum* in Virginia (Mecklenburg Co.), and (as larvae) on *S. bicolor* in New York (Tompkins Co.). It has been recorded from *S. altissima* (LeSage, 1986) and will feed on it in the laboratory, but appears rarely associated with this plant in the field.

(4) *O. sexvittata* (LeConte), *O. conferta* (LeConte), and *O. macrovittata* LeSage. LeSage (1986) lists *Solidago altissima, S. canadensis,* and *S. rugosa* as hosts for *O. conferta* and *Solidago* sp. for *O. sexvittata*; he had no host information for *O. macrovittata,* which he distinguished from *O. sexvittata* (with which it is sympatric in southeastern U.S.) by the breadth of the elytral vittae, the size of elytral punctures, and genitalic characters. *O. conferta* and *O. sexvittata,* which have effectively parapatric distributions in the north and south respectively, differ chiefly in the density and size of elytral punctures and in the intensity of pigmentation of the vittae. LeSage (1986) suggested that these two forms may represent geographical variation within a single species.

I have collected *O. conferta* on *Solidago altissima* in many localities in the northeastern U.S., on the closely allied *S. gigantea* in Tompkins Co., New York, and have observed it feeding on *S. juncea* (N.Y.: Livingstone Co.) and on *S. rugosa* (N.Y.: Suffolk Co.); it is most commonly associated with the *S. altissima* complex. *O. sexvittata* was collected in abundance on *S. altissima* in several parishes in Louisiana and in North Carolina, as well as on a related goldenrod, *S. leavenworthii,* in Florida (Dade Co.). A large sample of *O. macrovittata,* which LeSage (1986) described from 12 specimens from six southern states, was taken on *S. altissima* at Zwolle, Sabine Parish, Louisiana (18 May 1986), and another large collection, together with approximately equal numbers of *O. sexvittata,* was taken from a stand of the same plant five miles west of Starks, Calcasieu Parish, Louisiana.

Electrophoretically, *O. conferta* (New York) and *O. sexvittata* (Florida and Louisiana) differ significantly in allele frequency at three of 18 loci (Table 2A). Because allele frequencies vary geographically in many species, these data do not bear on the conspecificity of these forms, but their common host association and close morphological similarity suggest that they are conspecific. In contrast, electrophoretic data on *O. sexvittata* and *O. macrovittata* from the same locality (Starks, La.) bear on their status. Four of 18 loci are sufficiently polymorphic to test for allele frequency differences, and none differs significantly between individuals classified by elytral color pattern (Table 2B).

The density of elytral punctures was estimated on five specimens with the color pattern of *O. sexvittata* and ten with that of *O. macrovittata* from Dade Co., Florida and Sabine Parish, Louisiana, respectively, by counting the number of punctures intercepted by a linear microscope reticle at 50×. One anterior–posterior transect of 30 reticle units was taken near the base of the discal vitta, and two, of 50 units, were taken in mid-disc between the discal and subsutural vittae. For *sexvittata* and *macrovittata,* respectively, the mean numbers of punctures were 6.4 and 6.5 along the shorter transect, and 11.7 (SE = 0.538) and 9.9 (SE = 0.833) along the longer transects; the difference between the latter means is not significant ($t = 1.430$, df = 2, $P > 0.10$). Among other characters considered diagnostic by LeSage (1986), the breadth/length of the female sternum VIII did not differ (mean ± SE = 0.65 ± 0.029, 0.75

Table 2. Tests for allele frequency differences in *Ophraella conferta, O. sexvittata,* and *O. macrovittata.* Entries are number of genes scored.[1]

Locus	Taxon	Allele designation[2]			χ^2	df	*P*
A. *O. conferta* (N.Y.) and *O. sexvittata* (La. and Fl.)							
PGI		5	others				
	conferta	119	15		9.129	1	<0.005
	sexvittata	97	1				
PGM		3	7	others			
	conferta	107	15	8	131.293	2	<0.001
	sexvittata	1	65	12			
6PGD		2	13	others			
	conferta	1	209	8	72.558	2	<0.001
	sexvittata	32	73	13			
B. *O. sexvittata* (Starks, La.) and *O. macrovittata* (Starks, La.)							
PGM		7	9				
	sexvittata	50	8		0.263	1	>0.50
	macrovittata	58	7				
HK-1		3	others				
	sexvittata	48	9		0.018	1	>0.50
	macrovittata	60	12				
HK-2		6	others				
	sexvittata	51	7		0.969	1	>0.10
	macrovittata	71	11				
6PGD		13	others				
	sexvittata	35	21		0.039	1	>0.50
	macrovittata	47	26				

[1] E.C. designations of enzymes: PG1: 5.3.1.9; PGM: 2.7.5.1; 6PGD: 1.1.1.44; HK-1 and HK-2 (slow and fast loci, respectively): 2.7.1.1.

[2] Relative mobilities of electromorphs are as follows. The absolute position (in mm) on a typical gel is given in parentheses for the fastest of the designated electromorphs (relative mobility = 1.00). PGM *3* = 1.00 (30), *7* = 0.87, *9* = 0.73. 6PGD *2* = 1.00 (37), *13* = 0.95.

± 0.045 for *sexvittata* and *macrovittata,* respectively; $n_1 = n_2 = 3$; $t = 1.869$, $P > 0.10$); nor did the shape of the apical notch of this sclerite (highly variable), the form of the apex of the aedeagus, or the form of the spermathecal receptacle, which varies in *sexvittata* from rounded to "peanut-shaped" (LeSage, 1986), the form observed in all *macrovittata.*

Adult offspring were recovered from four female *O. macrovittata* and two *O. sexvittata* from Starks, Louisiana, that were enclosed individually in bags on *S. altissima* at Stony Brook, New York. The color pattern of the offspring of *sexvittata* (57 and 2 from the two females) conformed to that of *sexvittata,* but all four *macrovittata* segregated offspring of both patterns, as well as some that approached the *macrovittata* pattern but could not be readily classified. The proportions of *macrovit-*

tata + intermediate offspring were 0.86 (N = 30), 0.75 (N = 40), 0.64 (N = 14) and 0.57 (N = 7) in these broods. These data could be interpreted as reflecting a single locus with incomplete dominance, but provide no compelling evidence for this hypothesis, especially because females mate multiply (see below). The segregation, however, together with the foregoing observations, indicates that *macrovittata* and *sexvittata* represent a polymorphism for coloration, and that *Ophraella macrovittata* must be considered a junior synonym of *O. sexvittata.* Both LeSage (1986) and Balsbaugh and Hayes (1972), who referred *macrovittata*-like specimens to *O. conferta,* note that the elytral punctures are larger in "*macrovittata,*" and they impress me likewise. The coarseness of punctation may be a pleiotropic effect of genes governing pigmentation, because in *Ophraella* generally, the punctures included within the dark vittae tend to be larger than those not so included.

(5) *O. arctica* LeSage. This and the succeeding species appear very closely related, and constitute what I term the "communa group." Almost all the specimens on which LeSage based his description of *O. arctica* were collected on *Solidago multiradiata scopulorum* by W. J. Brown at Reindeer Depot, in the Mackenzie Delta north of Inuvik, Northwest Territories. I visited this region, 5–8 August 1987, and found neither the host plant nor beetles at Reindeer Depot, which has been abandoned and presumably has undergone succession since Brown's visit in 1948. I collected *O. arctica* in abundance on *S. multiradiata* at the southern edge of Inuvik, on a west-facing slope above the town dump; the hillside is recovering from a 1968 fire, and includes *Epilobium, Lupinus, Rosa, Salix,* and *Artemisia tilesii* among the dominant plants. During cold, wet weather, the beetles were collected from masses of litter taken from the base of the host plant.

O. arctica resembles *O. bilineata,* to which Brown referred at least some of his specimens (at University of California, Davis), but is smaller and darker, and differs in other characters noted by LeSage (1986). In addition, the elytral vittae of *O. bilineata* are more conspicuously free of punctures, and those bordering the vittae are more conspicuously enlarged; the border of tooth III of the mandible is finely serrate in *O. arctica* but does not appear so in *O. bilineata*; and *O. arctica* is fixed or nearly so ($p > 0.95$) at four electrophoretic loci (MPI, E.C.5.3.1.8; Aldolase, E.C.4.2.1.13; HK, E.C.2.7.1.1, faster of two loci; IDH, E.C.1.1.1.42, faster of two loci) for an allele found in *O. bilineata* and other members of the communa group at only a frequency of $p < 0.05$, if at all. Because *O. arctica* is apparently allopatric to all other species, its specific status cannot be determined with certainty at this time, but it is distinct enough to warrant specific status on a provisional basis.

(6) *O. bilineata* (Kirby). I have collected this form in abundance on *Chrysopsis villosa,* its only recorded host, at the following localities: Saskatchewan, 3 mi south of Chaplin; Alberta, southeast of Milk River, on Rte. 878 crossing the Milk River; Montana, 1 mi west of Cascade. Only those morphological characters noted by LeSage appear to distinguish *O. bilineata* from *O. communa.* At none of the 18 electrophoretic loci examined does *O. bilineata* carry a diagnostic allele with a frequency above 0.10, except at the fast IDH locus, at which an allele with high frequency (0.6) in *O. bilineata* was recovered at only low frequency in *O. communa* ($p = 0.08$ in New York) and in *O. notulata* ($p = 0.008$ in Florida). This same allele is fixed in the morphologically very distinctive *O. nuda.* Although LeSage lists records of *O. communa* from within the range of *O. bilineata,* I have not obtained *O. communa* in

that region and have no information on the possibility of gene flow between these closely related forms.

(7) *O. nuda* LeSage. This species was described from 26 specimens lacking host data. I found a dense population feeding and breeding on *Iva axillaris* on 17 July 1986 and 27 June 1987 on extensive dry mud flats at the southern edge of Pakowki Lake, 45 mi east of Milk River, Alberta, and smaller numbers on the same plant in the vicinity of Orion, 20 mi to the northeast. This species, reliably known only from southeastern Alberta, is very distinctive morphologically, differing from other members of the communa group by its sparse, short elytral pubescence, often yellowish elytral ground color, reduced subsutural vitta, rather uniformly sized elytral punctures, and depressed body form. Electrophoretically, it is fixed for an allele of PGM (E.C.2.7.5.1) and almost fixed ($p = 0.97$) for an allele of the fast HK locus, neither of which has been observed in any other species.

(8) *O. californiana* LeSage. This form is known almost entirely from the type series, collected from *Artemisia Douglasiana* at Drytown, California, 7 April 1974 by F. G. Andrews. I visited the type locality (F. G. Andrews, pers. comm.) on 9 July 1986 and 14 April 1987. The host plant is abundant both at this site and at several other California localities where collections were attempted, but no *Ophraella* were found, and no signs of feeding damage were evident. *Artemisia*-associated *Ophraella* appear to be very rare in this region.

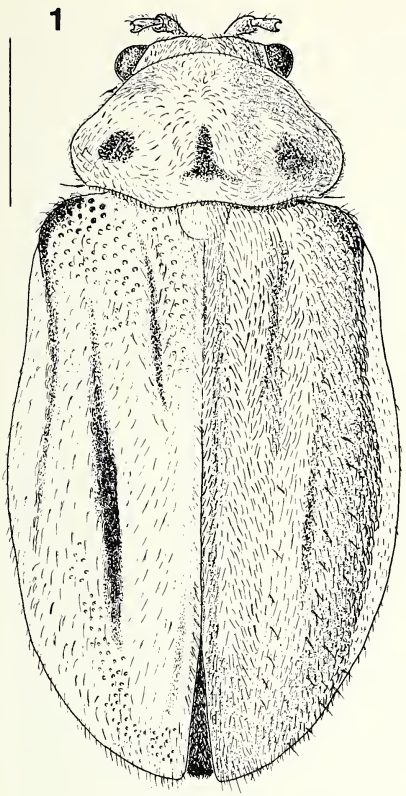
Another form of *Ophraella* has been found feeding on a different species of *Artemisia,* in western Texas. It occurs also in Arizona. This form differs sufficiently from *O. californiana* to warrant description as a new species:

(9) **Ophraella artemisia**, new species

Diagnosis. This species resembles *Ophraella californiana, O. communa,* and *O. bilineata* in habitus and the pattern of elytral vittae, but is distinguished from all of these by the more deeply emarginate border of the labrum and the convexly arched upper rim (molar region) of the mandible. It differs from *O. californiana* and *O. communa,* further, by the denser, more adpressed elytral pubescence comprised of shorter setae, and by the form of the pronotum, which is more convexly arched in cross section. The elytral punctures are smaller than those of *O. bilineata,* and it differs from this species and from *O. communa* in its host plant, *Artemisia Carruthii.*

Description of Imago. SIZE: Linear measurements (mean and standard error, in mm, N = 5 pinned females and 8 males from type series; measured with ocular micrometer): Total length (front of head to apex of elytra, in dorsal view) of females, 4.22 ± 0.083, of males, 3.66 ± 0.053; length of elytra (base of humerus to apex) of females 3.27 ± 0.076, of males 2.88 ± 0.041; width of pronotum of females 1.48 ± 0.027, of males 1.31 ± 0.027; pronotum length (along midline)/width of females 0.59 ± 0.017, of males 0.61 ± 0.010.

COLORATION: Ground color yellowish brown (testaceous), dorsally obscured by pubescence lending a gray appearance under most lighting; each elytron with four narrow pale to dark brown vittae, tending to black where darkest. Submarginal (lateral) vitta darkest at humerus, generally meeting subsutural vitta before apex, subsutural vitta becoming evanescent half to one-third the distance from the base. Discal vitta darkest at about midpoint of elytron, becoming obscure basally and



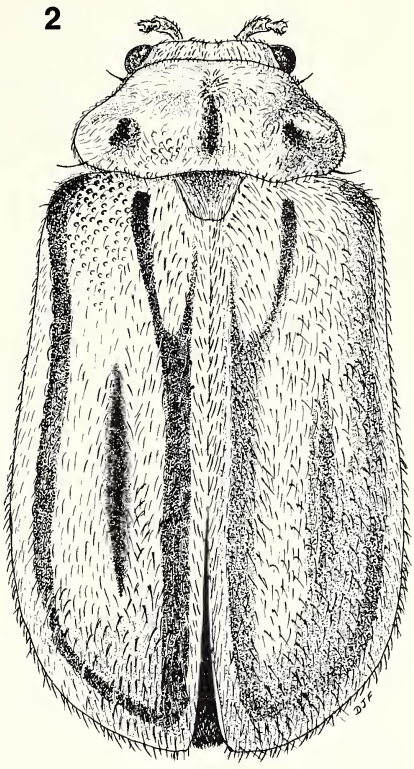


Fig. 1. *Ophraella artemisiae,* n. sp., female, paratype. Antennae and legs not fully portrayed.
Fig. 2. *Ophraella communa* LeSage, female. Canelo, Arizona, 11 Oct. 1955, G. D. Butler. Antennae and legs not fully portrayed.

apically. Supplementary vitta (LeSage 1986) originating and darkest near base, sometimes slightly carinate, oriented diagonally toward suture, sometimes joining subsutural vitta shortly distal to the latter's basal terminus, more often becoming evanescent before joining it (Fig. 1). Vittae in some specimens obsolescent, evident only in regions noted above as darkest. Pronotum with three small, dark brown maculae, obscure in some specimens; coronal suture of vertex, occiput, and in some specimens a broad dorsolateral extension from occiput toward margin of eye dark. Antennal segments dark brown, the bases of the six proximal segments testaceous. Clypeus pale; labrum with a dark brown transverse submarginal band, extended basad along sides and in midline; sclerites of mouthparts dark brown. Venter of mesothorax, metathorax, and abdominal sterna variably testaceous to piceous.

SETATION AND PUNCTATION: Body invested with pubescence, that of the elytra dense (at least three times as numerous as punctures) and moderately erect (at about 45° to surface); elytra with scattered, stouter, fully erect setae. Elytral punctures confused, dense, small, generally absent within darkest parts of vittae. Metepisternum densely invested with setae. Frontal tubercles not prominent, lacking setae.

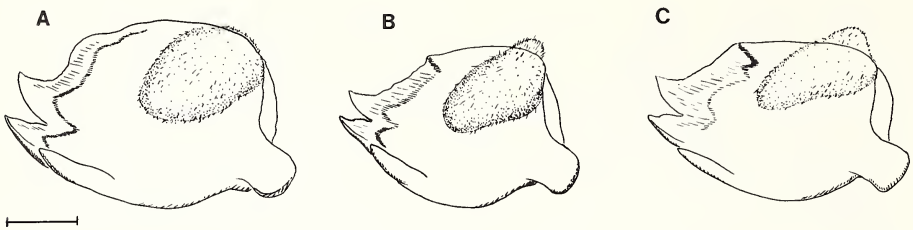


Fig. 3. Outline drawings of right mandible, in buccal view, of (A) *Ophraella artemisiae,* (B) *O. californiana,* (C) *O. communa,* all to same scale (bar = 0.1 mm). Drawn from female specimens. *O. artemisiae* and *O. californiana* were collected at their respective type localities; the specimen of *O. communa* was newly eclosed, reared from egg collected at Balmorhea, Texas. Length of elytron (for body size reference) of *O. artemisiae* 3.47 mm, of *O. californiana* 3.18 mm, of *O. communa* 3.94 mm.

OTHER STRUCTURAL FEATURES: Pronotum declining convexly from midline to lateral margin, surface almost even, eminence bearing lateral macula only slightly developed, rear margin only slightly concave. Anterior margin of labrum conspicuously, strongly concave; maxillary palpifer with three or four large setae; length of distigalea 1–1.5 times its width; upper margin (molar region) of mandible strongly convex, declining abruptly to the base of tooth III (Fig. 3); upper margin of tooth III generally but not always finely serrate; exterior surface of mandible bearing a small seta. Sternite VIII of female (LeSage, 1986) with moderately sclerotized lateral "wings," breadth across these slightly greater than length; breadth of its base 75% to 95% of its length. Spermatheca as in *O. californiana* and *O. communa,* apex simple or slightly produced. Genitalia of male, and of female except as noted, as in *O. californiana* and *O. communa.* Other characters as for the genus.

Type material. Holotype, female: Texas, Jeff Davis Co., 30°40′44″N, 104°01′41″W, on northwest slope of Mount Locke in the Davis Mountains at 1,870 meters (6,140 feet), on Texas route 118, 0.3 km (0.2 mi) south of road to Mount Locke peak and McDonald Observatory, Stefan P. Cover collector, 20 June 1987. Paratypes: Twelve specimens with data as for the holotype; 19 specimens from the type locality, D. J. Futuyma collector, 1 October 1988. Holotype (C. U. type number 6385) and 12 paratypes (collected 20 June 1987) deposited in the Cornell University Insect Collection, Ithaca, New York; 8 paratypes (collected 1 October 1988) in the Canadian National Collection, Ottawa, Ontario; 11 paratypes (same date) in the California State Collection of Arthropods, Sacramento; 6 paratypes (same date) in the American Museum of Natural History, New York.

Other material. Specimens in the collection of the Department of Entomology, University of Arizona, Tucson, as follows: "Ariz., Pima Co. Sta./Rita Mts., N end, Rose-/mont area, 31D48–53′N/110D42–47′W, 4400–/6175′ El., Anamax Mine/Inventory, 1975–1976/J. Busacca & C. Olson": 3 specimens, two bearing additional label "McCleary Cn./Sec. 30 5200′/9–23 1975 D-Vac," and one "Ridge Area/Sec 24 5600′/7–30 1975 D-Vac." "Catalina Mts./Ariz. 24 HkHy./July 18 1955/G. D. Butler," "Ceanothus fendleri" (1 specimen); "Blue Mts./Greenlee Co./VI-18-43 Ariz.," "M. puberula Blake?/F. H. Parker Collection" (1); "Hualpai Mtn. Pk./Mohave Co., ARIZ./

Aug. 9, 1962 6200'/F Werner, J Bequaert/Ceanothus fendleri" (1); "Walnut Ck, Sta Maria/Mts., Yavapai Co., AZ/4-IX-78 Hetz" (1); "Vic. Sunset Crater/Nat. Mon., Coconino/Co., ARIZ. VII-17-58/6500'. WL Nutting" (2). All these specimens have the distinctive pronotal form and emarginate labrum of *O. artemisiae,* and in all except the Greenlee Co. specimen, the elytral surface is obscured by dense, short, reflective pubescence. The vittae are rather faint to almost entirely obsolete in all. Dissection of one specimen from McCleary Cn., Sta. Rita Mts., Pima Co. and one from Sunset Crater Nat. Mon. revealed the diagnostic form of the mandible and the short distigalea in both. "*Ceanothus fendleri,*" noted on two specimens, is unlikely to be a host plant. See note added in proof for Minnesota records.

Host association. This species was abundant at the type locality on 1 October 1988, feeding and breeding on *Artemisia Carruthii* Wood (Asteraceae) (identification confirmed by B. L. Turner, University of Texas). Several larvae and old egg masses were observed. Upon return to the laboratory, on 5 and 6 October, feeding preferences of 21 wild-caught individuals were tested, after depriving them of food for 36 hr, by confining them individually with a fragment of each of three test plants (*Artemisia Carruthii, Ambrosia artemisiifolia, Helianthus ciliaris,* the latter somewhat desiccated). The beetles were observed for a total of seven hr over two days; on the first day, the first of two feeding attempts by each beetle was interrupted, so that a total of up to three feeding initiations was scored. All 21 beetles initiated feeding on *Artemisia,* 7 initiated at least one attempt on *Ambrosia,* and one consumed a slight amount of *Helianthus.* Of a total of 61 feeding attempts, 51 were on *Artemisia.* In contrast, of 18 *O. communa* collected from *Helianthus ciliaris* on the same date at Balmorhea, Texas (44 km NNE of the type locality of *O. artemisiae,* altitude 975 m) and similarly tested, none displayed any response to *Artemisia*; of 52 feeding initiations, 30 were on *Ambrosia* and 22 on *Helianthus.*

A trip to the type locality and environs on 14–15 July 1989 yielded few adults, one pupa (in a cocoon), several larvae, and eggs which may have been deposited in transit. The eggs were deposited singly in pits chewed into the plant surface, and so were partly enveloped by the plant's dense pubescence. The first eclosion of adults that developed from these eggs occurred on 15 August, the larvae having been reared on the host plant at 25°C, 15/9 L:D.

Diagnostic characters. O. artemisiae closely resembles *O. communa* LeSage (Fig. 2). LeSage (1986) refers to a "pale form" of *O. communa*; this may well include *O. artemisiae. O. artemisiae* differs from *O. communa* taken on *Helianthus ciliaris* at Balmorhea, Texas in the following respects: elytral vittae of *O. artemisiae* paler, the discal and supplementary vittae not extending as nearly to the base of the elytron, the supplementary vitta less often joining the subsutural; elytral pubescence somewhat shorter and denser, obscuring more of the elytral surface; pronotum more densely pubescent, more convex from side to side and with shallower impressions (the dorsal surface being more planar from side to side in *O. communa*); rear margin of pronotum generally less concave; anterior margin of labrum much more concave, labrum more intensely pigmented; distigalea shorter relative to width (at least twice its width in *O. communa*); upper margin of mandible convexly inflated (declining gradually to base of tooth III in *O. communa*: Fig. 3); margin of tooth III finely serrate in some *O. artemisiae,* not so in *O. communa*; seta evident on external surface of mandible, not so in *O. communa*; average size slightly less (elytral length of *O. communa* about

Table 3. Allele frequency differences between *Ophraella artemisiae* and a sample of *O. communa* taken on *Helianthus* at Balmorhea, Texas. Entries are numbers of genes scored.[1] All χ^2 values are significant at $P < 0.001$.

Species	Locus	Alleles[2]				χ^2 (df)
	MDH-1	1	2	5		
O. artemisiae		112	0	0		172.003 (2)
O. communa		0	14	46		
	IDH-1	1	7			
O. artemisiae		9	99			121.467 (1)
O. communa		57	3			
	IDH-2	1	2			
O. artemisiae		108	0			172.131 (1)
O. communa		0	64			
	LAP	5	6	others		
O. artemisiae		103	1	6		126.672 (1)
O. communa		5	53	0		
	6PGD	4	6	others		
O. artemisiae		27	72	0		32.193 (2)
O. communa		6	31	15		
	MPI	2	3	4 + 5	others	
O. artemisiae		0	17	83	12	71.440 (3)
O. communa		15	30	9	5	

[1] E.C. designations of enzymes: MDH-1 (anodal locus): 1.1.1.37; IDH-1 and IDH-2 (slow and fast loci respectively): 1.1.1.42; 6PGD: 1.1.1.44; MPI: 5.3.1.8.

[2] Relative mobilities of electromorphs (see footnote, Table 2): MDH-1 *1* = 0.80, *2* = 0.90, *3* = 1.00 (30). IDH-1 *1* = 1.00 (13), *7* = 0.46. IDH-2 *1* = 1.00 (20), *2* = 0.95. LAP *5* = 1.00 (52), *6* = 0.92. 6PGD *4* = 1.00 (20), *6* = 0.75. MPI *2* = 1.00 (55), *3* = 0.91, *4* = 0.96, *5* = 0.75.

3.6 mm in females, 3.1 mm in males). (Size, however, varies substantially with nutrition and other factors in *Ophraella* and is not a reliable character.) No genitalic differences are apparent. The form of the labrum and of the pronotum are the most evident characters by which most specimens can be distinguished without dissection. Electrophoretic comparison of 56 specimens of *O. artemisiae* and of 30 specimens of *O. communa* from Balmorhea, Texas revealed significant differences in allele frequencies at six loci (Table 3); the anodal malate dehydrogenase (MDH) and the faster of two IDH loci appear entirely diagnostic. (The alleles for which *O. artemisiae* appears fixed at these loci, and which do not appear in the Balmorhea sample of *O. communa* are, however, present in Californian samples referred to *O. communa*; the latter, in fact appear fixed for allele 1 at IDH-2. Samples of *O. communa* from New York, California, and Louisiana, like the Balmorhea sample, differ from *O. artemisiae* in their high frequency of MDH-1 alleles 2 and/or 5 and of IDH-1 allele 1, and in their low frequency of LAP allele 5.)

Specimens from several localities in Arizona, in the University of Arizona collection, conform to *O. communa* and are readily distinguishable from *O. artemisiae* by

the characters noted above. Five specimens from Holbrook, Arizona resemble *O. artemisiae* in that the vittae are pale to obsolete and the elytral pubescence is dense and reflective; structurally, however, these specimens conform to *O. communa.*

The specific status of *O. artemisiae* is considerably more ambiguous with respect to *O. californiana* LeSage, the only other *Ophraella* reported from a host in the genus *Artemisia.* Not only are the populations widely allopatric, so that differences could represent only intraspecific geographic variation, but no living material of *O. californiana* is available for electrophoresis or experimentation (e.g., on mating preferences). If geographically intervening populations are discovered, *O. artemisiae* might well prove to be a geographical variant of *O. californiana.* However, because the morphological differences between the two populations exceed those among several other taxa of *Ophraella* that are recognized as species (a criterion commonly applied to allopatric populations; Mayr, 1969), designation as a distinct species appears warranted at this time. The following comparison is based on close examination of four paratypes of *O. californiana,* and dissection of three of them, kindly provided for this purpose by F. D. Andrews (California State Collection of Arthropods, Sacramento). Based on LeSage's (1986) description and my own impression of the remainder of the specimens in C.S.C.A., Sacramento, these specimens are representative of the type series, at least in superficial characters.

O. californiae differs from *O. artemisiae* in the following respects: elytral punctures much larger, those between the discal and supplementary vittae more than 30% greater in diameter and about 70% greater in area than those of *O. artemisiae*; setae of elytral disc more procumbent (except for a few stouter, erect setae), sparser (only slightly more numerous than the punctures); dorsum of pronotum more coarsely and closely punctured; setae of metepisternum thicker and much sparser than in *O. artemisiae*; lateral wings of sternum VIII of female only slightly sclerotized, base of this sternum relatively narrower (up to 50% of length); anterior margin of labrum less concave; length of distigalea about twice its width; dorsal edge of mandible not convexly inflated, dropping gradually to base of tooth III (Fig. 3); upper edge of tooth III not serrate; no seta evident on exterior surface of mandible. Spermatheca, male genitalia, color pattern, and other features generally, as in *O. artemisiae.* The shape of the labrum and mandible (the latter requiring dissection), the size of the elytral punctures, and the density of the dorsal pubescence are the most diagnostic characters.

Larva. A small sample (3) of larvae of *O. artemisiae* is available at this time. I compare them here to larvae of *O. communa* from Long Island, New York (specimens from Texas or Arizona are not available for comparison), and of *O. bilineata.* The larvae of *O. artemisiae* and *O. communa* are indistinguishable with respect to the setation of the head capsule, the mouthparts, and the sclerites of the thorax and abdomen. The anterior margin of the labrum may be slightly more deeply emarginate in *O. artemisiae.* The only evident, slight, differences between the species are in pigmentation and in the shape of the mandible. The vittae of *O. artemisiae* are pale to obsolescent, those of *O. communa* being considerably darker. In *O. artemisiae,* the ventral border of tooth IV of the mandible (LeSage, 1986) is almost straight, and the apex of the tooth is blunt, almost truncate. The dorsal border of the mandible is slightly produced anteriorly, forming an acute angle with the base of tooth V, and is slightly sinuous anterior to the penicillus. In *O. communa,* tooth IV is acute and has a strongly convex lower margin; the dorsal rim rises convexly at an obtuse angle

from the base of tooth V, and is convex or straight from the apex to the penicillus. The three larvae of *O. bilineata* that I have examined are likewise indistinguishable from those of *O. artemisiae* except by their darker vittae and the form of tooth IV and the dorsal border of the mandible, which conform to the condition in *O. communa*. In *O. bilineata,* the dorsal edges of teeth II and III of the mandible are finely serrate, but are less conspicuously so, or not at all, in *O. artemisiae* and *O. communa*. The ratio of the depth to the length of the mandible in *O. bilineata* (mean = 0.72) is probably greater than in *O. artemisiae* (0.65) or *O. communa* (0.63). Larger sample sizes would be required, however, to be sure that any of these differences are diagnostic.

(10) *O. notulata* (Fabricius). LeSage (1986) applied the name *notulata* to the species that had hitherto been designated *integra* LeConte. Prior to LeSage's work, the epithet *notulata* Fabricius was applied to the species that LeSage has named *communa*.

I have collected this species on the salt marsh shrub *Iva frutescens* (=*I. oraria*) on both the Atlantic and Gulf coasts, and on the herbaceous annual *I. annua* in Louisiana. *O. notulata* and *O. communa* taken from, respectively, *I. annua* and *A. artemisiifolia* in a mixed stand in Baton Rouge, Louisiana were both electrophoretically and morphologically distinct. I cannot be certain that neither species occupied each other's host at this site. When these beetles were presented with a choice of these two plants in the laboratory, none of 10 *O. communa* fed on *I. annua,* whereas 8 of 10 *O. notulata* greatly or exclusively preferred *I. annua*. Baton Rouge animals of both species, offered a choice of *I. frutescens* and *A. artemisiifolia,* accepted both plants, although a larger fraction of *O. communa* (24 of 28) than of *O. notulata* (17 of 29) preferred (i.e., ate more) *Ambrosia*. Feeding responses and larval survival of *O. notulata* and *O. communa* on each other's host in New York are described by Futuyma (in press).

O. notulata differs from *O. communa* in electromorph frequencies entirely or almost entirely at several loci (MDH [anodal locus], IDH-1 and IDH-2, 6PGD, AAT [E.C.2.6.1.1, cathodal locus], LAP [E.C.3.4.11.-]). Morphologically it is distinguished by the several features noted by LeSage (1986), as well as by the lower number of setae on the prementum (one rather than two per side) and cardo (1–2 rather than 5–6). The elytral setae are shorter, more procumbent, and more uniform in direction, presenting a more "groomed" appearance.

(11) *O. communa* LeSage. This form is denoted *O. notulata* in the literature (e.g., Welch, 1978; Goeden and Ricker, 1985) prior to LeSage's revision. Populations morphologically referable to this species are distributed throughout most of North America, from southern Canada into Mexico. Although regional differences in electromorph frequencies exist (unpubl. data), samples from New York, California, Georgia, and Louisiana share many of the same alleles, and display, in polymorphic condition, peculiar multi-banded phenotypes at the 6-phosphoglycerate dehydrogenase locus (6PGD); these are provisionally interpreted as evidence of a gene duplication, and have been observed only in this species.

Throughout eastern North America, *O. communa* appears to be associated exclusively with *Ambrosia artemisiifolia*. In California, it has been taken on *A. psilostachya, Iva axillaris,* and *Xanthium strumarium* (all in tribe Heliantheae, subtribe Ambrosiinae) (Goeden and Ricker, 1985; R. Goeden, pers. comm.). I found it breeding on *Helianthus ciliaris* at Balmorhea, Texas, and J. Sullivan (St. Ann, Mo.; pers. comm.)

observed a specimen feeding on *Ratibida pinnata* in Missouri (both plants in subtribe Helianthinae). Morphological and electrophoretic differences between *O. communa* and other species are noted above.

INTERSPECIFIC DIFFERENCES IN IMMATURE STAGES

Eggs. Eggs of *Ophraella* are pale yellow when deposited, deepening to orange as they age. They are generally deposited in clusters on the host plant; however, *O. notata* usually lays eggs singly. (*O. artemisiae* may also have this habit.) The external morphology is rather uniform, but a few differences are evident among the species (Fig. 4). Compared to *O. communa* (Fig. 4A), the elements of the outer reticulum of the chorion are narrow in *O. notata,* and the junctures are elevated into slight projections (Fig. 4B); those of the inner reticulum are broad and within each fenestrum of the outer chorion, the peripheral fenestra of the inner chorion are much larger than the central fenestra. In *O. nuda* and *O. bilineata* (Fig. 4C, D), the inner fenestra are more uniform in size than in *O. communa* and other species, and in *O. bilineata* the inner reticulum is only slightly elevated. The ridges of the outer reticulum appear broader and deeper in *O. cribrata* and *O. conferta* (Fig. 4E, F) than in other species.

Larvae. These descriptions supplement those of LeSage (1986). The structural terminology follows Böving (1929). Only characters that vary among species and are visible without dissection are noted. Modal numbers of setae are given. The following description of the fully grown third (ultimate) instar larva of *O. communa* from New York will serve for comparison with other species. Each side of pronotal shield with 14 setae, 10 of which lie anteriorly and medially and 2 in a posteromedial field; dorsal sclerites (interior prescutal, interior scuto-scutellar) of meso- and metathorax fused across midline (as also on abdomen), each with 2 setae; thoracic posthypopleural sclerites with 2 setae; abdominal segments 1–7 with 1 interior scuto-scutellar, 4 epipleural setae; ventrally with at least one very small "presternal" seta anterior to sternellar sclerite. Ground color cream, three longitudinal, irregular dark vittae as follows: dorsal (from near midline to lateral border of interior scuto-scutellar sclerite), dorsolateral (from upper border of parascutal to upper border of epipleural tubercle), ventrolateral (fainter, surrounding hypopleural tubercles).

The larvae of *O. arctica, O. bilineata, O. notulata,* and *O. nuda* are structurally similar to *O. communa* in all these respects (as is *O. artemisiae*; see description above). Their color pattern is also very similar, but the dorsal vitta of *O. arctica* appears less intense than in *O. communa*; in *O. bilineata* the ventrolateral vitta is absent or interrupted, and is restricted to the region dorsal to the hypopleural tubercles; in *O. nuda* the dorsolateral and ventrolateral vittae are effectively confluent, interrupted only by the sclerite-bearing tubercles and nonpigmented spots anterior to the epipleural tubercles; the ventrolateral vitta extends to the lateral border of the parasternal sclerites. In *O. notulata* (northeastern specimens examined), the several vittae are effectively fused, and there is little interruption of pigmentation between the midline and the parasternal region. Because of variation in the intensity and extent of pigmentation, it is far from certain that these several species can be reliably distinguished as larvae.

In *O. notata, O. cribrata,* and *O. conferta,* the thoracic posthypopleural sclerites typically bear one seta, and ventral setae are absent anterior to the sternellar sclerites.

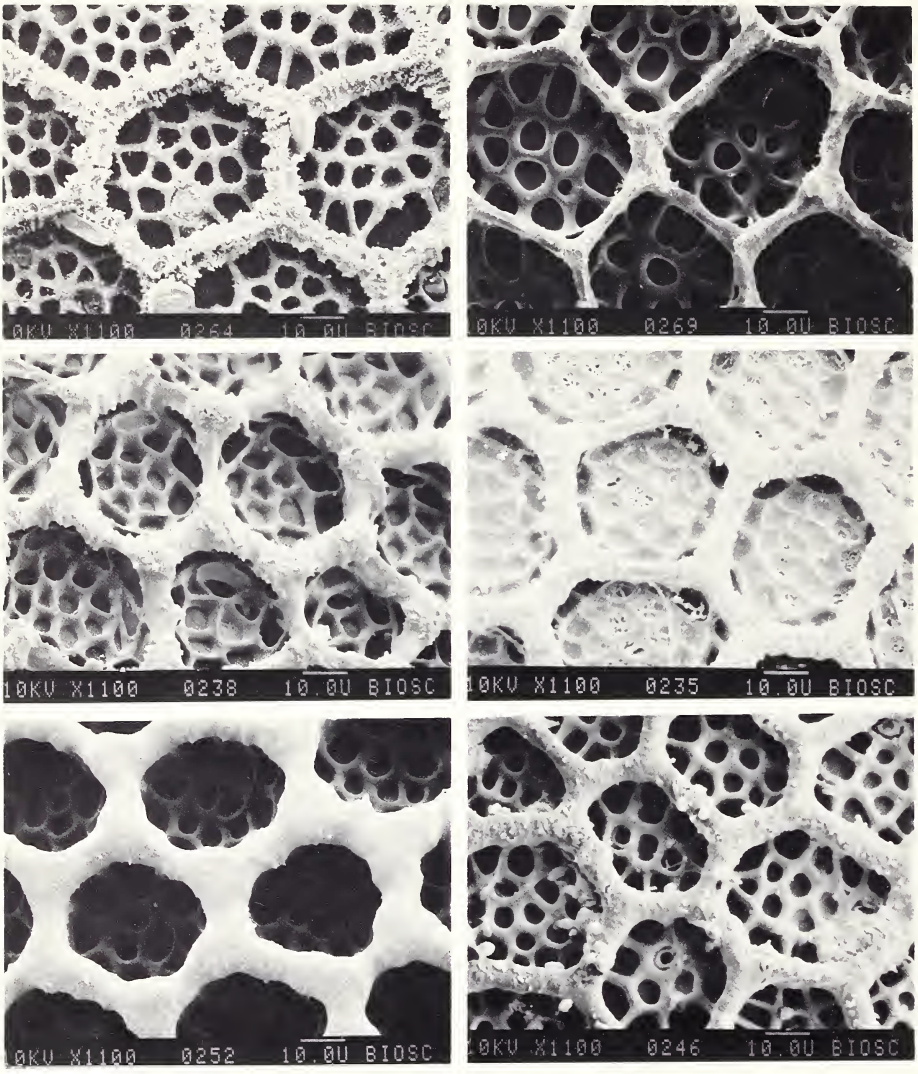


Fig. 4. Scanning electron micrographs of egg surface at 1,100×, taken normal to the surface approximately half way between micropyle and equator. Upper left to lower right: A. *Ophraella communa.* B. *O. notata.* C. *O. nuda.* D. *O. bilineata.* E. *O. conferta.* F. *O. pilosa.*

These species effectively lack pigmentation between the sclerites, which, especially in *O. notata* and *O. cribrata,* are paler than in the other species. The modal number of epipleural setae on the abdominal segments of *O. cribrata* is 5.

The larva of *O. pilosa* is most distinctive. The interior prescutal and interior scuto-scutellar sclerites are not, or hardly, fused at the midline, and setae are more numerous on the thoracic interior prescutal and interior scuto-scutellar sclerites (3 each), the

abdominal interior scuto-scutellar (2), the abdominal epipleural (5, as in *O. cribrata*), and the pronotal shield, with (modally) 19 setae, 16 of which lie in the anterior and lateral regions and 3 in the posteromedial field. The dorsal vitta consists of interrupted infuscations before and behind the sclerites; the dorsolateral vitta extends from the lower edge of the exterior prescutal to the lower edge of the parascutal; the ventrolateral vitta is obsolete.

Pupae. The following descriptions of the modal condition are based on 3–5 specimens of each species examined. Even in these small samples, the number and exact location of setae in each setal field is variable, except for those of the mesonotum, metanotum, and abdominal nota, which appear invariant. The vertical setae are also almost invariant. Much of the variation consists of apparent absence of setae, usually in the form of fluctuating asymmetry.

Pupae of *O. sexvittata,* which may be taken as a standard for comparison, conform to LeSage's (1986) figure except that the head bears, in addition to vertical and supraorbital setae, a pair of setae on the lower frons and a lateral pair (and in some specimens a medial pair also) on the labrum. The posterior discal region of the pronotum bears on each side either 3 or 4 setae, arranged in pairs, in addition to the 6 anterior and lateral setae figured by LeSage; the latter are not arranged into evident pairs. *O. cribrata* and *O. notata* are identical to *O. sexvittata,* although lower frontal setae were observed in no *O. cribrata* and in only one *O. notata. O. communa* consistently had 2 pairs of posterior discal setae on the pronotum, and 8 anterior and marginal pronotal setae, these arranged in pairs. No lower frontal setae were observed. Whereas the setal apices are complex, tending to bifurcate, in the preceding species, those of *O. communa* are mostly simple (acute or blunted), although a few are truncate to incipiently bifurcate. *O. notulata* and *O. nuda* are indistinguishable from *O. communa. O. pilosa* is most distinctive: the pronotum bears 5 posterior discal setae (a lateral pair and a medial triplet) and 11–12 marginal setae, not arranged in pairs but including a posterior marginal group of 3, rather than 2 as in *O. communa.* Each of the other nota bears an extra paramedial seta on each side, thus 3 on the meso- and metanota and 5 on each abdominal notum (rather than 2 and 4, respectively, as in all other species). Postorbital setae, otherwise observed only in two specimens of *O. nuda* (and asymmetrically present in these), are present but lower frontal setae are absent. The majority of setal apices are simple, but a considerable number are truncate to slightly bifurcate.

LIFE HISTORY AND BEHAVIOR

In the northeastern U.S., all species are found as adults in early spring; undoubtedly the adult is the overwintering stage in all species of *Ophraella.* Sperm were present in the spermathecae of *O. communa* and *O. conferta* collected in late autumn; thus females appear to store sperm over winter, as also reported for *O. communa* by Welch (1978) and Goeden and Ricker (1985). Both sexes mate repeatedly, and mating occurs throughout the season of activity. Eggs are laid on host foliage, generally in clusters (except in *O. notata*). As in *O. communa* (Welch, 1978; Goeden and Ricker, 1985), females lay a clutch of eggs every 1–3 days for several weeks. The development time of larvae before cocoon formation appears in all species observed to be approximately that recorded for *O. communa* by Welch (1978) and Goeden and Ricker

(1985) (i.e., 12–14 days at 27°C), but I have not taken careful data on the several species I have reared (*O. communa, O. notulata, O. notata, O. cribrata, O. conferta, O. sexvittata, O. pilosa*; cf. note on *O. artemisiae,* above). Adults and especially larvae appear to prefer fully expanded young leaves over mature foliage or leaves that have not yet expanded. Young larvae skeletonize the leaf, but adults eat through the leaf blade, including minor veins; species that feed on thick, succulent leaves (e.g., of *Iva*) leave feeding pits, generally on the abaxial surface. Especially in hot or sunny weather, the larger larvae and adults exhibit diel vertical migration, coming to the crown of the host plant during dusk and darkness; this behavior is especially notable in *O. pilosa, O. conferta, O. sexvittata,* and *O. cribrata,* but appears much less pronounced in *O. communa, O. notulata, O. bilineata,* and *O. notata.* During the day, adults of *O. pilosa, O. conferta,* and *O. notata* have been found resting within curled dead leaves near the base of the host plant.

All species have been observed to pupate within a cocoon, generally attached to foliage of the host or neighboring plants. In *O. communa, O. bilineata,* and *O. notata,* the cocoon is often on exposed foliage or among the branches of the inflorescence, but in other species pupation occurs most often near the ground. Pupae of *O. notulata* have been found not on the host, but within fragments of dead *Spartina* stems in nearby litter. Larvae of *O. communa* observed making cocoons displayed the behavior described by Goeden and Ricker (1985), with the following important exception: the viscous liquid material issues not from between the prothoracic legs, but from the anus. The larva curls the abdomen ventrally and forward, everts the rectum slightly, and strokes the everted rectum against the medial setae of the mesothoracic legs; a drop of liquid is then ejaculated and held between the prothoracic coxae, and the abdomen resumes its normal orientation. As described by Goeden and Ricker (1985), the larva periodically dips its mouthparts into the pool between the legs to obtain material for weaving. Analysis of dry cocoons of *O. communa* in a CHN Elemental Analyzer (Perkin-Elmer Model 240) gave approximately 10% N, 43% C, and 7% H by weight, oxygen presumably constituting much of the remainder. This analysis suggests that the cocoon is largely proteinaceous.

Table 4 summarizes the seasonal distribution of life history stages as I have found them in the field. Probably univoltine populations include *O. arctica, O. bilineata,* and *O. nuda,* as well as *O. conferta* and *O. cribrata* in New York. *O. notata* and *O. pilosa* appear bivoltine in New York, and *O. notulata* in the same region is at least bivoltine. *O. communa* is at least trivoltine on Long Island. The limited information from southeastern U.S. suggests that all species are multivoltine in this region.

Populations of species that feed on perennial plants appear to persist year after year; I have sampled from the same localized populations of all species (except *O. arctica* and *O. californiana*) for at least two, and in most cases four, years. Because *Ambrosia artemisiifolia* is annual, local stands often do not persist for more than one year, so *O. communa* populations associated with this host frequently must disperse. On one occasion, moreover, a stand of *Ambrosia* that harbored an abundant second generation of *O. communa* was, despite the seemingly good condition of the plants, virtually devoid of animals a month later, when a third generation was abundant in other local sites. This may indicate mass dispersal from stands of the host.

With respect to natural enemies, I have found dipteran larvae in the abdominal cavity of adults of *O. conferta* (collected 28 Sept., Ithaca, N.Y.) and *O. communa*

Table 4. Seasonal distribution of life history stages of *Ophraella* observed in the field. A, adult, E, egg, L1, first and/or second instar larva, L3, third instar larva, P, pupa. (1), (2) after locality indicate one or two visits to locality.

Species, location	March 15–31	April 16–30	May 1–15	May 16–31	June 1–15	June 16–30	July 1–15	July 16–31	Aug. 1–15	Aug. 16–31	Sept. 1–15	Sept. 16–30	Oct. 1–15	Dec. 16–31
arctica (N.W.T.) (1)									A, L3, P					
bilineata (MT, Alta., Sask.) (2)						A, E, L3, P		A	A, L3	A, P				
nuda (Alta.) (2)						A, E, L1, L3		A						
sexvittata (LA) (1) (S. Fl) (2)	A, L3			A, L3										A, E
conferta (NY, PA)			A, E	A, E	A	A, E, L1, L3		A, L3	A	A	A	A		
cribrata (NY)		A, E	A, L1, L3	A, L1, L3	A	A		A		A	A	A		
pilosa (NY)					A, E, L1	A, L1, L3		A		A, L3, L1, P		A		
notata (NY)			A	A	A, E			A, E, L1, L3	A, L1, L3	A, L1, L3, P		A, L3		
notulata (NY)		A	A, E	A, E	A, E, L1, L3		A, E, L1, L3, P	A, E		A, E, L1, L3	A, E	A, L3		
artemisiae (TX) (2)						A, E							A, L3	
communa (NY)				A, E, L1, L3	A, E, L1, L3	A, L3, P		A, E, L1, L3, P	A, E, L1, L3, P	A, E, L1, L3, P	A, L3, P	A, L3, P	A, P	
communa (TX) (1)													A, E, L1, L3, P	

(27 Sept., Long Island, N.Y.). Each parasitized beetle had one larva, and in female beetles, the ovaries and spermatheca had been consumed; fragments of the spermatheca were observed in one specimen. Too few specimens were dissected to provide an estimate of the rate of parasitism. Several *O. notata* (29 August, Ithaca, N.Y.) yielded fly puparia. A tachinid species (see second end note) emerged from *O. notulata* collected as larvae on *Iva frutescens* at Bluffton, South Carolina, 20 April 1989; the fly pupates within the beetle prepupa after it has formed a cocoon. Adult flies had emerged by 3 May. Tachinids have been reported from *O. communa* (Goeden and Ricker, 1985) and *O. bilineata* (LeSage, 1986). On Long Island, pupae of *O. communa* yielded a gregarious eulophid (Hymenoptera), identified by M. E. Schauff (Systematic Entomology Laboratory, U.S.D.A.) as *Asecodes* sp., near the Palearctic species *A. mento* Walker, which is known to parasitize the galerucine *Lochmaea suturalis* Thomson. *Asecodes* has not previously been formally recorded in North America (M. E. Schauff, in litt.). These parasitoids emerged from 15% of 141 pupae collected on 19 August 1986 at Stony Brook, New York, and were casually noted in material collected at other times.

Adult coccinellids (species not determined) have been observed feeding on eggs and pupae of *O. communa*. Adults of several species of *Ophraella* have been observed carrying larvae of the mite genus *Leptus* (Erythraeidae; identification courtesy of Dr. W. C. Welbourn, Ohio State University); heavy loads of these mites have been observed on *O. pilosa* near Ithaca, New York, and on *O. notulata* on Long Island, New York, in the autumn. Similar, perhaps conspecific, mites were observed on other beetle species and on Homoptera in the same sweep samples. These mites were tightly attached to their hosts by their mouthparts, and are unlikely to have been transferred among insects during sweeping.

SEXUAL ISOLATION

Exploratory tests of mating preference were performed for two geographical populations referred to the same species (*O. communa*) and for sympatric populations of reproductively isolated species (*O. communa* and *O. notulata*). In the former test, virgin adults were reared on *Ambrosia artemisiifolia* from eggs laid by *O. communa* collected 10 June 1988 on *Iva axillaris* at Antelope Spring, near Westgard Pass in the Inyo Mountains, Inyo Co., California. Virgin adults of *O. communa* from Stony Brook, New York, were reared from pupae collected on *A. artemisiifolia*. Virgin adults of both populations were fed *ad libitum* on *A. artemisiifolia* until testing, at which time the post-eclosion age was 7–14 days for the California population and 5–9 days for the New York population. On 4 August, 25 females from each population were individually confined in petri dishes, without food, with a California male and a New York male, the latter marked on one elytron with a dot of enamel paint. The dishes were placed on a lab bench under fluorescent lighting at 24°C, 68% R.H. and observed every 15 minutes for 6.5 hr. On 6 August, an additional 20 California females were similarly tested for 6 hr. Many females mated repeatedly (up to five times). No interactions among males were observed.

Levene's isolation index [I = (no. homogamic matings − no. heterogamic matings)/ total no. matings], which has an expected value of 0 for random mating and 1 for fully assortative mating, quantifies the departure from randomness. It is given with

Table 5. Mating trials. In each cell, the number of first and of total matings are above and below the diagonal, respectively. (A) Choice test, both sexes of *O. communa* from both California and New York, August 4, 1988. (B) Choice test, Californian female *O. communa* with male *O. communa* from California and New York, August 6, 1988. (C) Choice test, *O. notulata* and *O. communa* from New York, August 1987. (D) No-choice test, *O. notulata* and *O. communa* from New York, June 1988.

A. *communa* female from	Mated with male from	
	CA	NY
CA	14	9
	22	18
NY	1	24
	6	49

B. *communa* female from	Mated with male from	
	CA	NY
CA	13	5
	17	14

C. Female	Mated with male	
	notulata	*communa*
notulata	7	2
	10	4
communa	0	9
	0	16

D. Female	Mated with male	
	notulata	*communa*
notulata	5	7
	5	14
communa	0	8
	0	12

its standard error (see Wasserman and Koepfer, 1977). On 4 August (Table 5A), there was significant departure from randomness for both first matings ($\chi^2 = 18.019$, $P < 0.001$; $I = 0.583$, SE = 0.1172, $P < 0.05$) and for all matings ($\chi^2 = 21.655$, $P < 0.001$; $I = 0.495$, SE = 0.089, $P < 0.05$). This result was attributable chiefly to New York females, which mated almost exclusively with New York males. On 6 August (Table 5B), first matings by California females were marginally homogamous ($\chi^2 = 3.556$, $0.05 < P < 0.10$; $I = 0.440$, SE = 0.132, $P < 0.05$), but total matings were not ($\chi^2 = 0.290$, $P > 0.50$; $I = 0.97$, SE = 0.179, n.s.). Combining the results for all California females, first matings were marginally significantly homogamous ($\chi^2 = 4.124$, $P < 0.05$), but total matings, again, were not ($\chi^2 = 0.690$, $P > 0.50$). Two California females that had mated only with New York males laid eggs that subsequently hatched. All New York females that mated with California males also

mated with New York males, so the fertility of this interpopulation cross was not estimated.

In August 1987, virgin adults were reared from larvae of *O. communa* (on *Ambrosia artemisiifolia*) and *O. notulata* (on *Iva frutescens*), both from Stony Brook, New York. Ten female *O. communa* and 15 female *O. notulata* were individually confined with a male of each species for two hours for each of three days over a week's span, and observed every 15 minutes. Both first matings ($I = 0.78$, SE = 0.148, $P < 0.05$) and total matings ($I = 0.73$, SE = 0.124, $P < 0.05$) were significantly nonrandom, and no matings between female *O. communa* and male *O. notulata* were observed (Table 5C). In 1988, these observations were extended with virgins of both species collected in Stony Brook, New York (*O. notulata* reared from field-collected larvae, *O. communa* collected as pupae). Their post-eclosion age was 7–14 days for *O. notulata* and 2–6 days for *O. communa.* Females were not offered a choice of males. Ten of each of the two heterospecific combinations and 8 of each of the homospecific combinations were set up on two days (29 and 30 June); the same individuals were used on both days, but mixed into different combinations on 30 June. Observations were made every 15 minutes for a total of 16 hr. Undoubtedly because of the small sample sizes, no significant departure from randomness was observed either for first matings ($I = 0.30$, SE = 0.213) or total matings ($I = 0.096$, SE = 0.179; Table 5D). However, as in 1987, no female of *O. communa* mated with male *O. notulata.* Female *O. notulata* engaged in, if anything, more heterospecific matings. It is possible that the males of *O. notulata* were less competent to mate than those of *O. communa.*

These experiments on allopatric, presumably conspecific, populations and on closely related species show that some elements of mating discrimination exist between taxa associated with different host plants. Therefore, whatever role divergence in host association may play in the speciation of specialized phytophagous insects (Bush, 1975; Diehl and Bush, 1984; Futuyma and Mayer, 1980; Futuyma and Peterson, 1985), mating on the host plant is not the only potential basis for reproductive isolation.

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NOTES ADDED IN PROOF:

1. S. Y. Strauss (1987, *Ecology* 68:1670–1678) described "*Ophraella* sp." as an abundant specialist on *Artemisia ludoviciana* Nutt. at the Cedar Creek Natural History Area, Bethel, Anoka County, Minnesota. Twelve specimens from the collection of the Cedar Creek Natural History Area, sent to me by J. Haarstad, conform to *Ophraella artemisiae* in all features, including the diagnostic features of the mouthparts. All are labelled "U.S.A., MINNESOTA/

Anoka County/Cedar Creek Natural/History Area," with dates 2 June–10 Sept., 1985–1989. Notations on the labels, "Artlu" and "AS," indicate specimens hand-picked and swept, respectively, from *Artemisia ludoviciana* (J. Haarstad, pers. comm.). Four specimens have been deposited in the Cornell University Insect Collection. *Artemisia ludoviciana* and *A. Carruthii,* the known hosts of *O. artemisiae,* are in the same section (Abrotanum). *A. ludoviciana* is native to prairies and dry soils from southern Ontario and Missouri to British Columbia and northern Mexico, and is naturalized on the east coast from Quebec to Virginia (M. L. Fernald, *Gray's Manual of Botany,* 1950). Thus *O. artemisiae* undoubtedly has a broader distribution than is known at present.

2. The tachinid reared from *Ophraella notulata* collected at Bluffton, S.C., 20 April 1989, has been identified as *Celatoria* sp. by D. Grimaldi (American Museum of Natural History). The two North American species of *Celatoria* are known to parasitize four other genera of Galerucinae (Arnaud 1978, U.S.D.A. Misc. Publ. 1319).

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